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ORIGINAL ARTICLE

No sensitive period for the development of individual face learning in *Polistes fuscatus* wasps

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Abstract

Social isolation often has lasting negative effects on social behavior, but less research has tested how the timing of isolation influences its effects. Some behaviors have a sensitive period where experience has particularly strong effects, while other behaviors are more flexible. Here, we test how the timing of social experience influences the development of individual face learning in *Polistes fuscatus* wasps. Individual face recognition is a key aspect of communication in wasps, so wasps reared in a typical environment are adept at individual face learning. We reared wasps in 5 treatments that differed in the timing and amount of social experience: 14 days isolation, 14 days nest, 7 days nest, 7 days nest then 7 days isolation, and 7 days isolation then 7 days nest. Then, we tested individual face learning. Experience with conspecifics improved individual face learning, but the timing of experience did not impact performance. Wasps reared in normal social environments were adept at learning and remembering faces, while isolated wasps were unable to learn and remember faces. Early isolation did not have a stronger effect than later isolation, indicating that there is no early sensitive period for face learning in paper wasps. Instead, paper wasps exhibit a high level of plasticity in the development of individual face learning. Overall, this work emphasizes the role of plasticity in the development of complex social recognition and offers insight into the conditions where evolution favors high plasticity over rigid sensitive periods in development.

Significance

Animal behavior is influenced by experience during development. In some cases, the timing of an experience is important. In other cases, development is flexible such that experiences at any time have similar effects on behavioral development. We alter the amount and timing of social experience in wasps to test whether wasps have an early sensitive period where social experience has a particularly strong effect on capacity for individual face learning. We find that social experience improves wasps' ability to learn and remember the unique faces of other wasps, but the timing of experience doesn't influence performance. Wasps isolated early and late in life perform similarly. Therefore, early social experience is not necessary for individual face learning.

Keywords Plasticity · Sensitive period · Face recognition · Neural development · Individual recognition · Learning

Introduction

A sensitive period occurs when the effect of an experience on the brain is particularly strong for a limited time during development (Knudsen 2004). For example, barn owls have a sensitive period during which visual experience influences the development of their auditory space map. Owls can readily adjust the auditory space map early in life, but lose this flexibility as they age (Brainard 1998). Critical periods are a special class of sensitive periods that occur when information provided by an experience is required for normal development and experience alters behavior permanently

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(Scott 1962; Fawcett and Frankenhuis 2015). Filial imprinting in goslings and other birds is a classic example of a critical period, where chicks form a permanent attachment to a moving stimulus in the hours following emergence from the egg (Lorenz 1935). Sensitive periods have been found in diverse taxa and contexts, but less is known about why sensitive periods occur (Fawcett and Frankenhuis 2015).

The type and extent of sensitive periods vary widely across taxa and contexts (Knudsen 2004; Mueller 2018). Development can be highly plastic such that there is no sensitive period and experiences throughout life have similar effects on an animal's phenotype. Alternatively, development may be less plastic such that experiences during a sensitive period have stronger effects on an animal's phenotypes. For example, many songbirds have defined sensitive periods during which they learn their song via exposure to the songs of adult tutors (Marler 1970; Gobes et al. 2019). Other songbirds are not limited by a sensitive period and can learn new songs throughout their lives (Beecher and Brenowitz 2005).

Behaviors involved in social interactions may be particularly likely to develop during sensitive periods. Social experience is typically important for the development of normal social behavior (Taborsky and Oliveira 2012). As a result, social isolation affects both neural development and adult behavior in diverse taxa (Boulay and Lenoir 2001; Tunbak et al. 2020; Wang et al. 2022; Xiong et al. 2022). Often, socially isolated individuals are less socially competent than individuals reared in a typical social environment. Individuals who have been isolated display affiliative and aggressive behavior inappropriately (Mauduit and Jeanson 2023; Taborsky and Oliveira 2012) or respond differently to social communication than individuals with normal social experience (Keesom et al. 2017; Tibbetts et al. 2019). Social isolation can also influence cognitive ability, with social deprivation often reducing performance on tasks like learning, memory, and spatial orientation (Lambert and Guillette 2021). Fewer studies have tested how the timing of social isolation influences behavior. Some work indicates that there are sensitive periods where isolation has relatively strong effects on adult behavior (Cairns et al. 1985; Hol et al. 1999). Other work has found that the effects of isolation are flexible and reversible (Leser and Wagner 2015).

Individual face recognition is a complex and environmentally responsive social behavior. As a result, it is the type of behavior that may have a sensitive period for its development. Face recognition is an important aspect of social interactions in taxa including humans, some non-human primates, a cichlid fish, dogs, sheep, and *Polistes fuscatus* paper wasps (Kendrick et al. 2001; Huber et al. 2010; Parr 2011; Wang and Takeuchi 2017; Tibbetts et al. 2021). It is difficult to experimentally test how social experience influences the capacity for face recognition in many taxa given the challenge of altering social experience in a humane and realistic manner. Nevertheless, some research suggests experience facilitates the development of face recognition. For example, humans with poor vision due to congenital cataracts have impaired face processing (Le Grand et al. 2003). Human recognition of other-race faces is low when individuals lack experience with other race faces and improves with increasing experience (De Heering et al. 2010; Tanaka et al. 2004). In *Polistes fuscatus* paper wasps, there is direct experimental evidence that experience influences face learning. Wasps with more social experience are more adept at learning and remembering conspecific faces than wasps with less social experience (Pardo-Sanchez et al. 2022; Pardo-Sanchez and Tibbetts 2023). Thus far, we lack experiments testing whether there is a sensitive period during which social experience has a particularly strong effect on the development of face recognition.

This study experimentally tests whether *Polistes fuscatus* paper wasps have a sensitive period for individual face learning. Paper wasps have highly variable facial patterns that are used for individual face recognition. Individual face recognition plays an important role in minimizing aggression and maintaining social hierarchies on and off nests (Tibbetts 2002; Tibbetts et al. 2020). Similar to humans, *P. fuscatus* use specialized face recognition mechanisms like holistic processing to facilitate face learning (Pardo-Sanchez and Tibbetts 2023; Tibbetts et al. 2021a; 2021b). Previous work indicates that social experience influences individual face recognition. Wasps raised in a normal social environment with multiple conspecifics excel at individual face recognition, while socially isolated wasps are unable to individually identify conspecifics (Tibbetts et al. 2019c). Wasps raised with one conspecific have an intermediate capacity for individual face learning (Pardo-Sanchez and Tibbetts 2023). Previous work has not tested whether the timing of social experience influences individual face learning development.

We experimentally altered the amount and timing of social experience in *Polistes fuscatus* workers to test whether wasps have a sensitive period for conspecific face learning. Wasps were reared in 5 different treatment groups. Two groups were raised on their nest, one for 14 days (14 nest) and one for 7 days (7 nest). One group was raised in isolation for 14 days (14 isolated). The last two groups spent 7 days on a nest and 7 days in isolation, but the order of social experience differed between groups. One group was on a nest for 7 days followed by isolation for 7 days (7 nest + 7 isolated). The other group was isolated for 7 days followed by being on a nest for 7 days (7 isolated + 7 nest). If social experience influences performance, we predict that wasps with more social experience will learn faces more accurately than wasps with less social experience. If the timing of social experience influences performance, performance will differ in wasps who are isolated for the first week and wasps who are isolated for the second week. Reduced individual face learning in wasps isolated during the first week supports a sensitive period during the first week of worker development. Reduced individual face learning in wasps isolated during the second week suggests that recent exposure is important for facial learning.

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Methods

Treatment groups

We collected *P. fuscatus* individuals and their nests near Ann Arbor, Michigan, U.S.A. Following collection, the nests and associated wasps were housed in clear plastic containers (5 inches wide x 8 inches long x 7 inches high) under a natural day/night cycle and given ad libitum water, sugar and *Galleria mellonella*, *Hermetia illucens*, and *Spodoptera exigua* caterpillars. Wasp larvae are naïve to complex visual stimuli, individual recognition, and social hierarchies upon eclosion from the pupal case because they are immobile and have rudimentary eyes used primarily for light and motion detection (Gilbert 1994). We checked each nest daily for adults newly eclosed from pupation. Adults that eclosed between the daily next checks were painted with distinctive marks on their wing tips before being placed in their treatment group. Wasps from 31 different nests were used in the experiment:14 nest ($n=19$, 15 nests), 7 nest ($n=19$, 12 nests), 14 isolated ($n=16$, 6 nests), 7 nest + 7 isolated ($n=18$, 12 nests), 7 isolated + 7 nest ($n=15$, 10 nests).

Wasps in the nest treatment group were returned to their natal nest. Wasps in the isolation treatment group were housed in plastic deli cups with sugar, caterpillars, water, and small pieces of paper for nest building. Isolation and nest wasps were kept in the same environmental chamber with the same day/night cycle. The wasps in the 7 isolated and 7 nest groups were transferred back to their natal nest after being in isolation for 7 days. Conversely, the wasps in the 7 nest and 7 isolated groups were taken off of their nest and put into isolation after staying on their nest for 7 days. Wasps from the 7 nest group remained in their treatment group for 7 days before being trained. Wasps from the 14 nest and 14 isolation groups remained in their treatment groups for 14 days before being trained. While on nests, wasps interacted with a minimum of five adult conspecifics. There was no difference in performance between wasps housed on small nests (5–10 individuals) and wasps housed on larger nests (10 + individuals) ($F_{2,66}=1.2$, $p=0.27$), consistent with previous work showing that wasps reared in small groups readily develop the capacity for individual face learning (Pardo-Sanchez et al. 2022). *Polistes* wasps are considered mature 5 days after eclosion, participating in standard adult behavior like flying, hunting, navigating, and competitive and cooperative behavioral interactions among conspecifics (Giray et al. 2005; Shorter and Tibbetts 2009). Previous work has shown 7 day old *P. fuscatus* wasps excel at individual face learning (Tibbetts et al. 2022).

Face training and testing

The wasps were trained to differentiate between pairs of *P. fuscatus* faces using previously established methods (DesJardins and Tibbetts 2018; Tibbetts et al. 2019b, c). Face images used for training were photographs of *P. fuscatus* from Michigan (see Supplemental Fig. 1). Wasps were trained on one of three unique pairs of stimuli. The particular image that was correct was swapped across trials and was not linked with performance in this study ($F_{5,47}=0.89$, $p=0.50$) or in previous work using the same method (DesJardins and Tibbetts 2018; Tibbetts et al. 2019b, c). All face images were printed at life size using a commercially available Sony Picture Station photo printer.

We trained and tested the wasps' ability to discriminate between a neutral face stimulus and a negative face stimulus (Fig. 1). Previous work has shown that the ability to learn and remember individual wasp faces during training is linked with individual recognition capacity. Within and between species, wasps that are capable of individual recognition can learn and remember wasp faces during training, while wasps that are not capable of individual recognition are unable to learn and remember wasp faces (Sheehan and Tibbetts 2011; Tibbetts et al. 2018b, 2019a). For example, *P. metricus*, socially isolated *P. fuscatus* from MI, and *P. fuscatus* from central PA are not capable of individual recognition in social situations and are unable to learn to discriminate wasp faces during training (Sheehan and Tibbetts 2011; Tibbetts et al. 2019b, 2021a). In contrast, *P. fuscatus* from MI and NY are capable of individual recognition and readily learn to discriminate faces (Sheehan and Tibbetts 2011; Tibbetts et al. 2018b). Caste differences in individual face recognition are also reflected in different individual face learning performance. Nest-founding queens are more adept at individual recognition during social interactions than workers and also learn to discriminate individual faces more accurately than workers (Tibbetts et al. 2018a). Therefore, individual face learning performance provides useful information about capacity for individual face recognition.

Wasps were trained by placing them in a 2.5 × 4 × 0.7 cm wood and Plexiglas box with six identical face images glued to the inside walls (Fig. 1). In half of the training trials, the

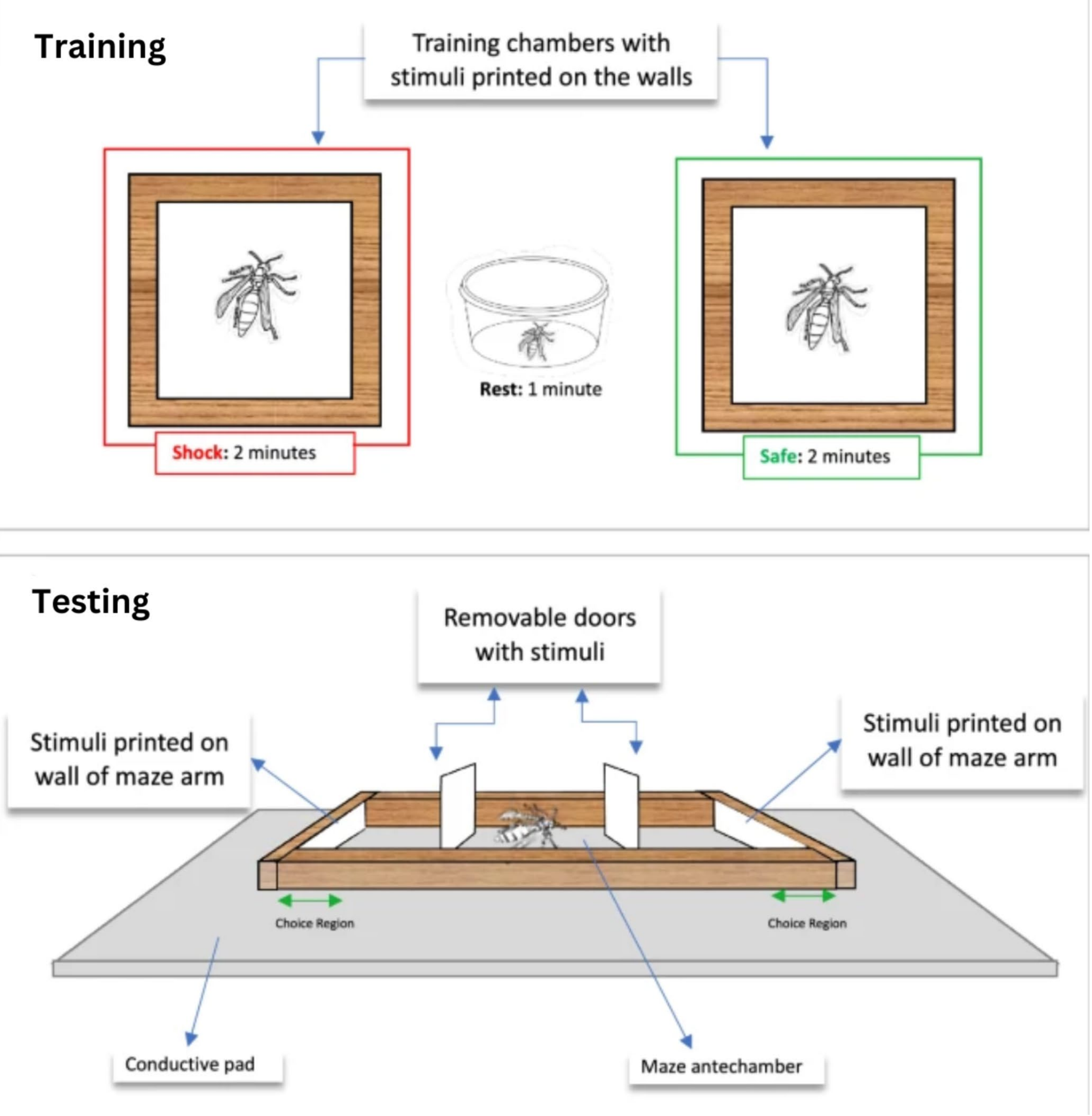

Fig. 1 Wasp training and testing methods. **Training**: Wasps are trained in small chambers with facial stimuli on walls. Wasps were placed in chambers with incorrect facial stimuli while receiving a mild electric shock. Wasps were then placed into chambers with correct facial stimuli with no electric shock. **Testing**: Wasps were tested in a rectangular chamber with the correct face image on one door and the incorrect face image on the other door. The same face image was present on the far wall of the respective sides of the chamber. Once in a neutral position, doors were removed. Learning was assessed by measuring which stimulus the wasp approached over 10 trials. Stimuli location was switched between trials to ensure wasps responded to stimulus rather than location. Figure modified from (Weise et al. 2022)

wasp was placed in a box with negative stimuli and received a mild electric shock from an electrified pad for 2 min. The electrified pad was made of antistatic conductive foam electrified by two copper wires connected to a Variac transformer. In the other half of the bouts, wasps were placed in a similarly sized box with neutral faces and the pad was not electrified for 2 min. Between each bout, wasps were given a 1 min break in a darkened holding container with a water source. For example, a wasp trained to discriminate between faces A and B would first be placed in the container with face A while receiving a shock for 2 min. The wasp would then be removed and given a 1 min break in a holding container. Then, the wasp would be placed in the container with face B while not receiving a shock for 2 min, followed by another 1 min break. This process is repeated 5 times per wasp so that the wasps see each face 5 times.

After training, the wasp was given a 45 min break in a holding container with water. Then, learning was assessed by measuring whether the wasp approached the correct or incorrect stimuli over 10 trials. Testing occurred in a 3 × 10 × 0.7 cm rectangle that was not electrified (Fig. 1). One end of the rectangle had the correct stimuli and the other end of the rectangle had the incorrect stimuli. The center of the rectangle had two removable partitions that confined the wasp. One partition had the correct stimulus on it while the other had the incorrect stimulus. At the beginning of each trial the wasp was placed in the center of the rectangle between the clear partitions. Once the wasp was in a neutral position, both partitions were removed simultaneously, and the wasp was free to walk through the rectangle. Wasps that learned typically turned towards the correct stimuli while confined in the center of the rectangle. When the partitions were removed, the wasp quickly walked towards the correct stimuli. A wasp was scored as making a choice when its head and thorax moved beyond the partition placed 2.5 cm from each end of the rectangle. After a wasp made a choice, it was removed from the rectangle and given a 1 min break in a holding container with water. The placement of the neutral and negative stimuli (right or left side) was determined randomly and changed between trials. This ensured that wasps did not associate a particular direction with correct choices. Each wasp completed 10 trials.

Statistical analysis

Analyses were performed in SPSS v. 28. We compared learning across wasps using a general linear model. The dependent variable was the number of correct choices (out of 10). The independent variable was the wasp treatment group: 14 isolated ($n = 16$), 14 nest ($n = 19$), 7 isolated + 7 nest ($n = 15$), 7 nest ($n = 19$), and 7 nest + 7 isolated ($n = 18$). Wasps were obtained from 31 different nests, with the same nest providing workers for multiple treatment groups. Nest ID was originally included as a subject variable in the statistical model, but was removed from the final model because it did not explain variation in individual face learning. We ran one analysis including wasps from all treatment groups and a separate analysis including only those wasps with 7 days of experience on a nest (7 nest, 7 isolated + 7 nest, 7 nest + 7 isolated). We used Fisher's Least Significant Differences post-hoc pairwise analyses to compare learning between treatment groups. We used binomial tests to assess how performance in each treatment group differed from the 50:50 random expectation. The binomial test provides an exact test of whether the number of correct versus incorrect choices differs from the 50:50 random expectation. Binomial tests provide p-values with no test statistics.

Results

Rearing environment affected wasps' performance, as the number of correct choices differed between treatment groups (Fig. 2; $F_{4,82} = 4.9$, $p < 0.001$). Post-hoc pairwise analyses in Table 1 show that social experience improves individual face learning. However, there is no difference in performance between wasps that experienced early versus late isolation.

Among wasps that experienced 7 days of social interaction on the nest, the timing of the experience influenced performance (Fig. 2; $F_{2,49} = 3.4$, $p = 0.041$). Post-hoc pairwise analyses show that wasps that spent their entire 7 day life on a nest performed better than 14 day old wasps that spent 7 days on a nest followed by 7 days in isolation ($p = 0.012$). However, there is no difference in performance between 7 day old wasps that spent their entire life on a nest and 14 day old wasps that spent 7 days in isolation followed by 7 days on a nest ($p = 0.33$). There was also no difference between 14 day old wasps that spent 7 days in isolation followed by 7 days on a nest and 14 day old wasps that spent 7 days on a nest followed by 7 days in isolation ($p = 0.15$).

Binomial tests show that wasps reared in the 14 nest group ($p < 0.001$), 7 nest group ($p = 0.002$), and the 7 isolated + 7 nest group ($p = 0.041$) learned to differentiate between the face images, as they chose the correct face image more often than expected by chance. However, wasps in the 14 day isolation ($p = 0.81$) and 7 nest + 7 isolated ($p = 0.72$) did not perform better than expected by chance.

Discussion

Our results indicate that social experience influences individual face learning in *Polistes fuscatus* wasps, but there is no early-life sensitive period for face learning. Wasps with more social experience are more adept at individual face learning than wasps with less social experience. However, early life social experience does not have a stronger effect on performance than later life social experience. In fact, recent social experience may have a stronger positive effect on performance than early-life social experience. Wasps that were isolated for 7 days then reared with conspecifics for 7 days learned to discriminate faces more accurately than expected by chance. However, wasps that were reared with

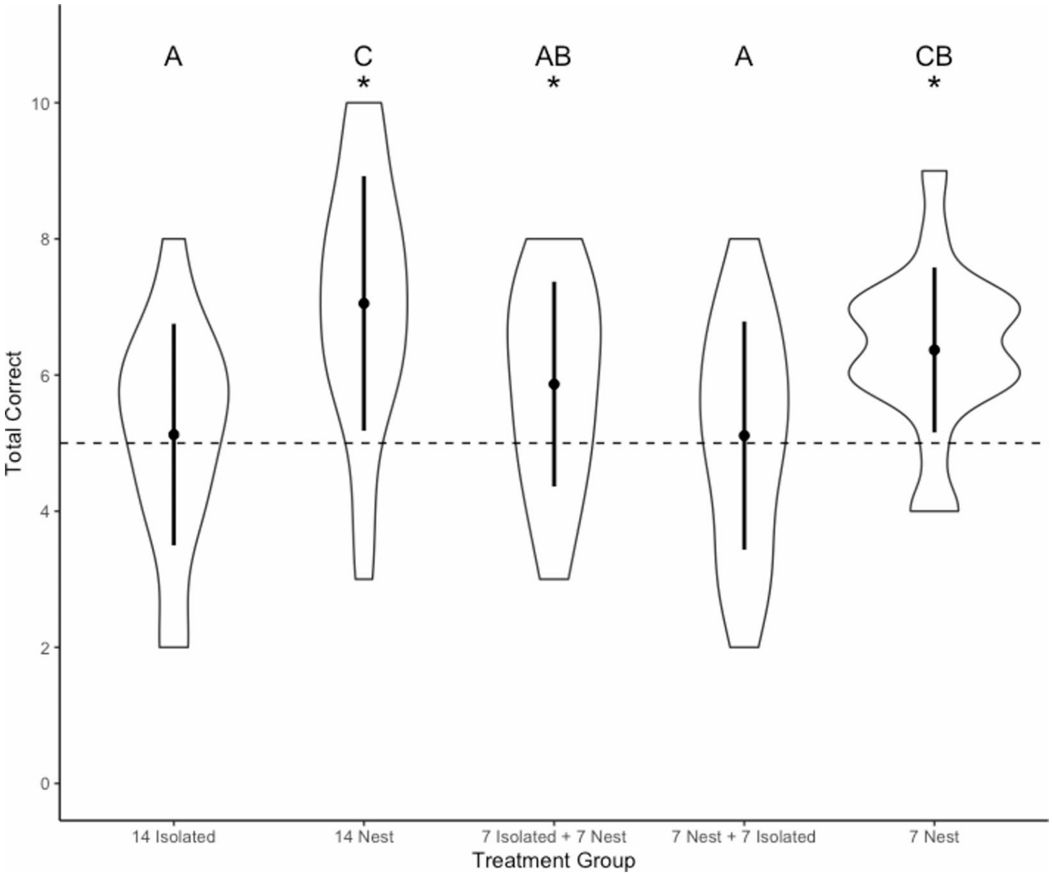

Fig. 2 Correct choices out of 10 in wasps trained to discriminate between pairs of *P. fuscatus* faces. Wasps were reared in one of the following environments: 14 days isolated, 14 days on a nest with conspecifics, 7 days isolated followed by 7 days on a nest, 7 days on a nest followed by 7 days isolated, and 7 days on a nest with conspecifics. *Indicates treatment groups that learned to discriminate faces more accurately than was expected by chance. Dotted line represents 50:50 random expectation. Different letters denote significant differences between groups in post hoc analysis. Dots and lines reflect means and ±2 standard deviations. for max and min. Violin plots show the density of scores for each treatment group

Table 1 Summary of posthoc comparisons between the treatment groups. Bold indicates significant differences

	14 nest	7 nest	7 isolation + 7 nest	7 nest + 7 isolation
7 nest	0.19			
7 isolation + 7 nest	**0.034**	0.36		
7 nest + 7 isolation	**<0.001**	**0.019**	0.18	
14 isolation	**<0.001**	**0.024**	0.20	0.98

conspecifics for 7 days then isolated for 7 days did not discriminate faces more accurately than expected by chance, suggesting they may lose some capacity for individual face learning during isolation.

It was initially surprising to find that wasps do not have an early sensitive period during which social exposure influences their capacity for individual face learning. This study involved a relatively long period of isolation for a wasp. *P. fuscatus* workers are behaviorally mature at 5 days and the average lifespan for a worker is approximately 30 days. As a result, we initially expected 7 days of early life isolation would influence performance. Early sensitive periods often influence performance on complex, social tasks like face recognition (Zeanah et al. 2011). For example, some work suggests humans may possess a sensitive period for the development of facial processing until ages 10–12, though the human face processing system also appears to have a high degree of flexibility (Pascalis et al. 2020). Monkeys may also have a sensitive period for face learning because early, short-term social experiences produce long-lasting effects on face processing (Sugita 2008). Sensitive periods also occur in other types of social communication, including bird song (Marler 1970) and parent-offspring recognition (Bolhuis 1999).

Wasps may have a flexible capacity for individual face learning because there may be an evolutionary incentive to remain flexible when the developmental environment varies (Cini et al. 2019).Wasps usually eclose from pupation onto a nest full of other wasps and gain ample social experience as they mature. However, wasps occasionally experience social isolation when they eclose onto nests that were abandoned during the pupal period. Wasps that eclose onto an abandoned nest can gain social experience later in life if they join the aggregations of wasps from multiple nests that form before and after diapause (Dapporto & Pelagi 2006; Laub et al. 2024a). The capacity to learn and remember individuals during social interactions is beneficial in *P. fuscatus*. Individual recognition reduces conflict and increases cooperative behavior (Sheehan and Tibbetts 2009; Laub et al. 2024b). As a result, having the flexibility to develop individual face learning later in life may be beneficial. The flexibility development of individual face learning in wasps is consistent with previous work in other taxa that suggests the developmental window for learning can be prolonged if animals are deprived of information (Hensch 2004; Linkenhoker et al. 2004; Michel and Tyler 2005). For example, zebra finches exposed to adult song tutors do not normally learn songs when they are older than 65 days old, but finches who are isolated from hearing tutors extend their song learning period (Gobes et al. 2019).

Much of the previous work on sensitive periods has focused on the neural processes that occur over development to produce sensitive periods. Some research suggests that sensitive periods in development are common because neural circuits are more flexible early in life and maintaining plasticity later in life may be costly or difficult (Knudsen 2004; Thomas and Johnson 2008). As a result, a loss of neural and behavioral flexibility over time may be widespread. However, this study found that behavioral flexibility for individual face learning persists over the wasps lifetime, suggesting that neural development in *Polistes* is flexible and early changes in brain development may be reversible with different experience. Much previous work has shown that social insect brains change with both age and experience (da Silva et al. 2023; Farris et al. 2001; Gandia et al. 2022; Gronenberg et al. 1996). Further, social isolation alters social insect neural development. For example, social isolation changes gene expression and brain development in bumblebees (Wang et al. 2022) and fire ants (Manfredini et al. 2022), as well as antennal lobe volume in ants (Goolsby et al. 2024). *P. fuscatus* wasps that are socially isolated have smaller anterior optic tubercle, a visual glomerulus, than socially reared *P. fuscatus* (Jernigan et al. 2021). The results of this study suggest that isolation-induced neural changes may be reversible with subsequent experience, though additional experiments will be important to understand the type and extent of neural plasticity that underlies the behavioral flexibility identified in this study.

Sensitive periods in social insect recognition have been studied most extensively in the context of nestmate recognition. Historically, social insects were thought to have a sensitive period soon after eclosion from pupation during which they learned the colony-specific nest odor (Gamboa et al. 1986; van Zweden and d'Ettorre 2010). However, more recent work indicates nestmate recognition is more flexible and adjusts in response to a changing social environment (Boulay and Lenoir 2001; Couvillon et al. 2007; Signorotti et al. 2014). For example, *Polistes dominula* wasps can form a template of nestmate odor during adulthood rather than relying on odor exposure immediately after eclosion from pupation (Cappa et al. 2020). As a result, there is growing evidence that strict sensitive periods in the development of recognition may be relatively uncommon.

The results of this study indicate that social isolation at any point in life may have negative effects on individual face learning. Wasps housed with conspecifics for 7 days then isolated for 7 days had lower capacity for individual face learning than wasps that were never isolated. Social isolation has diverse negative effects on animal phenotypes, including health, stress, social competence, and competitiveness (Bailey and Moore 2018; Yadav et al. 2024; Xiong et al. 2023). Experiments often test the effect of early isolation on development, but isolation at any point in a social animal's lifespan may have negative effects (Apfelbeck and Raess 2008; Begni et al. 2020; Brandão et al. 2015). Additional work that explicitly tests the effects of isolation throughout the lifespan will be important to understand how the amount and timing of isolation influences animal phenotypes.

Overall, our study shows that social experience is important for the development of individual facial learning in paper wasps. However, the timing of the social experience does not have a strong effect on performance, as there is no early sensitive period for individual face learning in paper wasps. Instead, either early or late social experience enables wasps to develop the capacity for individual face learning. Therefore, the development of complex social behaviors like face learning are surprisingly plastic. Future work that tests the plasticity of neural and genetic underpinnings of individual face learning in wasps, as well as recognition studies in a broader array of taxa, will help identify how and why developmental plasticity is maintained.

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Data availability Data are uploaded as supplemental material.

Declarations

Competing interests The authors have no competing interests to declare that are relevant to the content of this article.

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